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**Ornis Hungarica 2026. 34(1): 408–422.**
DOI: 10.2478/orhu-2026-0029

# Reproductive stages effects on nest morphology and reproductive success of Yellow-legged Gull on Oued Charef Dam Island, Northeast Algeria

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*Received: June 08, 2025 – Revised: February 21, 2026 – Accepted: February 27, 2026*

Boukrouma, N. 2025. Reproductive stages effects on nest morphology and reproductive success of Yellow-legged Gull on Oued Charef Dam Island, Northeast Algeria. – Ornis Hungarica 34(1): 408–422. DOI: 10.2478/orhu-2026-0029

**Abstract** Understanding how reproductive stages influence avian reproduction is essential for predicting species' responses to environmental variability. While much research has focused on temperate ecosystems, studies in semi-arid and Mediterranean environments remain scarce. In these regions, reproductive stages defined by key environmental conditions such as rainfall patterns and food availability are often less predictable and more strongly influenced by resource availability than by temperature. This study presents the first in-depth investigation of how reproductive stages affect nest morphology and reproductive success in a Yellow-legged Gull population inhabiting the small island of Oued Charef Dam, northeastern Algeria. Reproductive activity was monitored across four distinct stages: early breeding, mid-breeding I, mid-breeding II, and late breeding. Key nest morphological traits (external and internal diameters, nest depth) and reproductive parameters (egg size, volume, and weight; clutch size; hatching and breeding success) were measured throughout these stages. My findings reveal significant variation in nearly all traits across reproductive stages, with the lowest values observed during early breeding and the highest reproductive investment occurring in late breeding. Clutch size was the only trait that did not vary significantly. Multivariate analyses, including Principal Component Analysis (PCA) and Redundancy Analysis (RDA), showed that reproductive stages explain a substantial proportion of the variation in both nest structure and reproductive traits, highlighting a gradient of increasing reproductive investment from early to late stages. These results underscore the importance of breeding stage timing in shaping reproductive strategies in unpredictable environments and provide valuable baseline data for an under-studied region. In the context of climate change and increasing environmental uncertainty, understanding how birds adjust their breeding investment across reproductive stages is critical for informing future conservation strategies.

Keywords: reproductive stages, nest morphology, reproductive success, principal component analysis (PCA), redundancy analysis (RDA)

**Összefoglalás** Annak megértése, hogy az ökológiai szezonalitás hogyan befolyásolja a madarak szaporodását, alapvető fontosságú a fajok környezeti változékonyságra adott válaszainak előrejelzéséhez. Míg a legtöbb kutatás a mérsékelt égövi ökoszisztémákra összpontosított, a félsivatagi és mediterrán környezetben végzett vizsgálatok továbbra is ritkák. Ezekben a régiókban az évszakok gyakran kevésbé kiszámíthatóak, és a csapadék és az erőforrások elérhetősége erősebben befolyásolja őket, mint a hőmérséklet. Ez az első olyan tanulmány, amely részletesen vizsgálja, hogy az évszakok hogyan befolyásolják a fészekmorfológiát és a szaporodási sikert az Algéria északkeleti részén található Oued Charef Dam szigeten élő sárgalábú sirály populációban. A szaporodási aktivitást négy különböző ökológiai fázisban követtem nyomon: a költés előtti időszakban, a tojásrakás, a kotlás és a fiókanevelés időszakában. A fészek legfontosabb morfológiai jellemzőit (külső és belső átmérő, fészek mélysége) és a szaporodási paramétereket (tojás mérete, térfogata és tömege, fészekalj mérete, kikelési és szaporodási siker) a költési szezon során folyamatosan mértem. Eredményeim jelentős szezonális eltéréseket mutatnak majdnem minden tulajdonság tekintetében, a legalacsonyabb értékeket a költés előtti szakaszban, a legmagasabb reproduktív befektetést pedig a fiókanevelés során figyeltem meg. A fészekalj mérete volt az egyetlen olyan tulajdonság, amely nem változott szignifikánsan az évszakok között. A többváltozós elemzések (PCA és RDA) azt mutatták, hogy az ökológiai szezonalitás magyarázza mind a fészekszerkezet, mind a szaporodási jellemzők változásának jelentős részét, és a költés előtti időszaktól a fiókanevelésig a növekvő befektetés egyértelmű gradiensét mutatják. Ezek az eredmények kiemelik a szezonális időzítés fontosságát a szaporodási stratégiák kialakításában kiszámíthatatlan környezetben, és értékes alapadatokat nyújtanak egy kevéssé vizsgált régióból. Az éghajlatváltozás és a növekvő környezeti bizonytalanság összefüggésében a jövőbeli természetvédelmi erőfeszítések szempontjából kritikus fontosságú annak megértése, hogy a madarak hogyan igazítják reproduktív befektetéseiket az évszakok között.

Kulcsszavak: ökológiai szezonalitás, fészek morfológia, költési siker, főkomponens analízis (PCA), redundancia analízis (RDA)

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# Introduction

Seasonality plays a fundamental role in shaping the timing and intensity of reproductive investment across bird species (Verhulst *et al.* 1997). In many temperate zone birds, environmental factors such as temperature, day length, and food availability vary predictably across seasons, resulting in distinct periods of high and low reproductive success (Verhulst *et al.* 1995). This has led to the evolution of synchronized breeding patterns, where reproductive effort is concentrated during windows of optimal resource availability. Numerous studies have shown that such seasonal variation affects a wide range of reproductive parameters, including clutch size, egg dimensions, nest construction, and chick survival (Verhulst 1995, Jetz *et al.* 2008). Nests initiated too early or too late in the breeding season tend to exhibit reduced egg size, smaller clutch sizes, and lower chick survival compared to those initiated during periods of peak food availability (Durant *et al.* 2007). Overall, these patterns support the view that birds strategically adjust reproductive investment in response to environmental cues to maximize fitness under changing seasonal conditions.

However, most existing research focuses on temperate ecosystems where climatic seasonality is strongly defined. Much less is known about how variation across reproductive stages influences reproductive traits in tropical and subtropical environments. In these regions, seasonality may be less related to temperature and more driven by rainfall patterns, resource pulses, or habitat quality (Nwaogu *et al.* 2018). Tropical birds often display greater flexibility in their breeding schedules, and their reproductive strategies may be less tightly constrained by fixed seasonal windows (Heenan *et al.* 2015). A significant knowledge gap remains regarding the combined effects of different reproductive stages on nest morphology and reproductive output. While several studies have documented changes in one or two traits across the breeding cycle, comprehensive analyses integrating multiple parameters such as nest structure, egg size, clutch size, and reproductive success remain rare, especially in tropical and semi-arid systems (Capilla-Lasheras *et al.* 2017b).

Within this broader context, the Yellow-legged Gull (*Larus michahellis* Naumann, 1840) offers an interesting model species for addressing these questions. It is a large seabird distributed widely along the Mediterranean coastline and on nearby islands (Spelt *et al.*

2021). The species typically breeds in dense colonies on rocky cliffs, islands, or occasionally in urban areas, constructing nests using vegetation, debris, and locally available materials (del Hoyo *et al.* 2014). Reproduction generally spans from late winter to early summer, with clutch sizes usually ranging from two to three eggs (Baaloudj *et al.* 2014). Yellow-legged Gulls also exhibit flexibility in breeding timing, adjusting reproductive schedules to local environmental conditions that can influence reproductive success and chick survival (Boukrouma *et al.* 2021). Characteristics of the nest site – such as exposure, elevation, and substrate play important roles in determining reproductive outcomes by affecting egg viability and chick protection (Monaghan & Nager 1997, Angehr *et al.* 2014).

Located in northeastern Algeria, the island within Oued Charef Dam represents a unique ecological transition zone influenced by both Mediterranean and Saharan climates. The site experiences hot, dry summers and mild, wetter winters, with irregular rainfall concentrated between October and March (300–400 mm annually). Vegetation is sparse and dominated by drought-resistant herbaceous plants and low shrubs. The rocky, semi-open terrain provides suitable nesting habitat for colonial waterbirds, while fluctuating water levels shape foraging opportunities. To date, only one prior study has examined breeding gulls at Oued Charef Dam (Boukrouma *et al.* 2021), and no research has systematically evaluated how variation in reproductive stages affects morphological and reproductive parameters in this population.

To fill this gap, this study provides the first comprehensive assessment of how reproductive stages influence reproductive traits in a wild bird population from this island. I focus on four key reproductive stages (early breeding, mid-breeding I, mid-breeding II, and late breeding), and use a combination of univariate and multivariate analyses to examine their effects on nest dimensions, egg size, clutch size, and overall reproductive success. I hypothesize that reproductive investment is lowest during early breeding due to environmental or physiological constraints and increases through laying and incubation to peak during chick rearing, when fitness benefits are maximized. Understanding how reproductive investment varies across these stages is particularly important as global climate patterns continue to shift, potentially affecting the timing and predictability of breeding cycles (Capilla-Lasheras *et al.* 2021a, McRae 2024).

## Material and Methods

### Study area

The study was carried out on a small rocky island (approximately 150 ha) located within the Oued Charef Dam (36°5’22.91”N, 7°23’20.78”E; altitude: 920 m; reservoir surface area: 1010 ha), near the town of Souk Ahras, in northeastern Algeria (Boukrouma *et al*. 2021) *(Figure 1)*. The area experiences a semi-arid Mediterranean climate characterized by an annual precipitation ranging from 158 mm to 480 mm, with over 70% of rainfall occurring during the winter months (October to March). Mean annual temperatures fluctuate between 11.9 °C and -22 °C, with hot dry summers and cold winters. Seasonal variation is pronounced, with a dry period lasting from late spring through early autumn (Boukrouma *et al.* 2021).

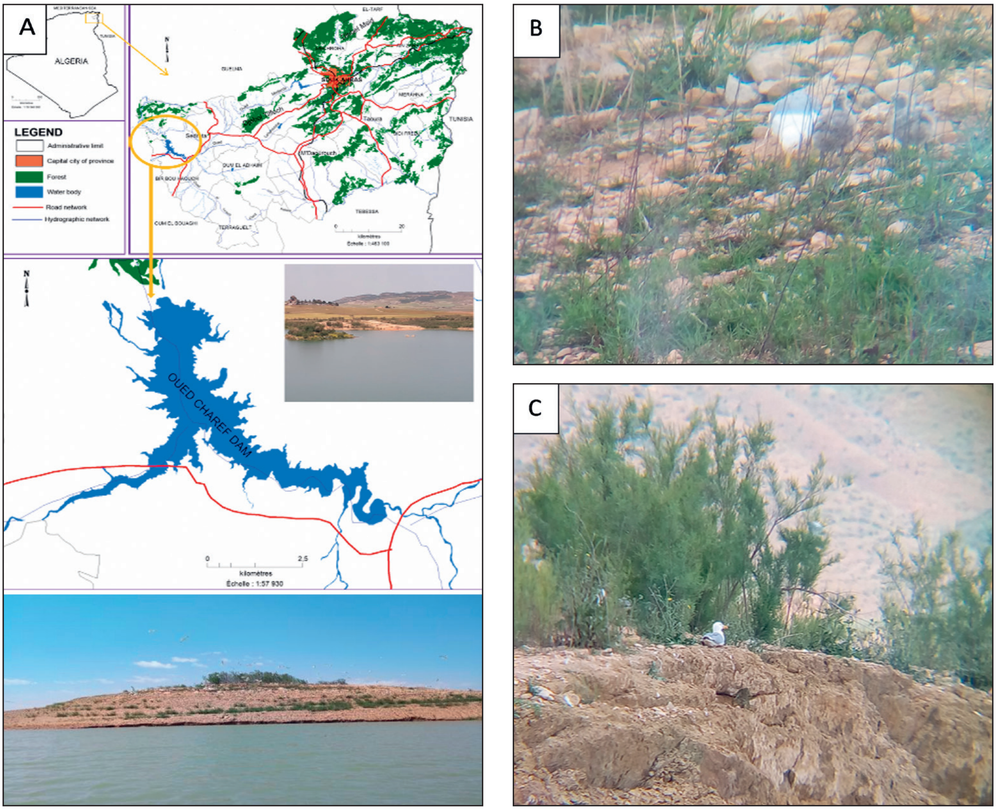



*Figure 1.* (A) Map showing the location of the study area: a small rocky island within the Oued Charef Dam, located near the Province of Souk Ahras, Northeastern Algeria (Map adapted and recreated from data published in Analele Universității din Oradea, Fascicula Biologie, Boukrouma *et al.* 2021). (B) Adult Yellow-legged Gull *(Larus michahellis)* feeding two chicks on the island. (C) Yellow-legged Gull incubating eggs in a nest during the incubation period on the same island

*1. ábra* (A) A vizsgálati terület elhelyezkedését bemutató térkép: egy kis sziklasziget az Oued Charef Sam-on belül, Souk Ahras tartomány közelében, Északkelet-Algériában. (B) Öreg sárgalábú sirály *(Larus michahellis)* két fiókát etet a szigeten. (C) Tojásokon kotló sárgalábú sirály a fészekben

## Data collection and nest monitoring

Field surveys on the Yellow-legged Gull were conducted from early January to early June 2019. Nest structure was measured, including internal and external diameters and nest depth, using a measuring tape, and weekly nest checks were performed to monitor clutch progress, chick productivity, and nesting success. To account for temporal variation, the reproductive period was divided into four stages (early breeding (early January – mid-February), mid-breeding I (mid-February – early March), mid-breeding II (early March – late April), and late breeding (late April–early June), each representing roughly one-fourth of the fieldwork period. While this classification is based on calendar dates rather than direct physiological or behavioral markers, it provides a practical framework to analyze temporal changes in reproductive traits. Nest success was determined from direct observations of hatching or the presence of eggshell fragments and down feathers, and nests were considered failed if all eggs disappeared or were damaged before hatching (Boukrouma *et al.* 2021). Chick productivity was monitored up to 20 days post-hatching. Cases of egg loss due to cannibalism were identified through direct observation or the presence of peck marks and yolk traces near nests. Each egg was individually marked, weighed using a Pesola spring scale (0–500 g, precision 1 g), and measured for length and width to the nearest 0.1 mm, with egg volume was calculated using the formula: Volume = 0.51. $LB^2$, where L is the maximum length and B is the maximum breadth. The coefficient 0.51 is the species-specific shape coefficient for gull eggs, as established by Hoyt (1979). Fresh egg weight (W) was estimated using the relationship $W = K_W LB^2$, where $K_w$ is a species-specific constant determined from published data (Hoyt 1979). Laying dates were defined as the date the first egg was laid, and for nests found during incubation, the laying date was estimated by subtracting a 28-day incubation period from the hatching date (Chokri *et al.* 2023). Nest outcomes were categorized as successful (at least one egg hatched), abandoned (no activity observed, eggs cold or disappeared), or predated (evidence of egg or chick predation) (Monaghan & Nager 1997). I acknowledge that these categories may oversimplify complex outcomes, as abandoned nests may have experienced undetected predation and successful nests may still have partial egg or chick loss, which should be considered when interpreting reproductive success.

**Statistical analysis**

All statistical analyses were carried out using R software, version 4.5.0 (R Core Team 2025). Prior to analysis, data were checked for normality using the Shapiro–Wilk test in order to determine the appropriate statistical approach for each variable. To evaluate the influence of ecological season on morphological and reproductive traits, one-way ANOVA was employed when the data met assumptions of normality and homogeneity of variances. This allowed for the comparison of means across the different reproductive stages. Post-hoc Tukey's HSD tests were then used to identify which specific seasonal pairs differed significantly, offering detailed insights into temporal patterns. For traits that did not meet the assumptions of parametric testing, non-parametric alternatives such as the Kruskal–Wallis test was applied, followed by Dunn's post-hoc test with Bonferroni correction to identify pairwise differences among reproductive stage. This approach ensured robust comparisons across groups without violating statistical assumptions. To examine broader patterns and interactions among multiple variables simultaneously, multivariate analyses were also conducted. Principal Component Analysis (PCA) was used to reduce dimensionality and identify the main axes of variation in the dataset, helping to visualize how nest and reproductive traits varied across ecological seasons. Additionally, Redundancy Analysis (RDA) was implemented to assess the extent to which reproductive stages explains variation in the multivariate structure of the data. These methods together provided a comprehensive understanding of how seasonality shapes reproductive strategies and nest morphology. Boxplots were generated using R packages "ggplot2" selected for his capacity to produce high-quality and interpretable figures suited to ecological data.

## Results

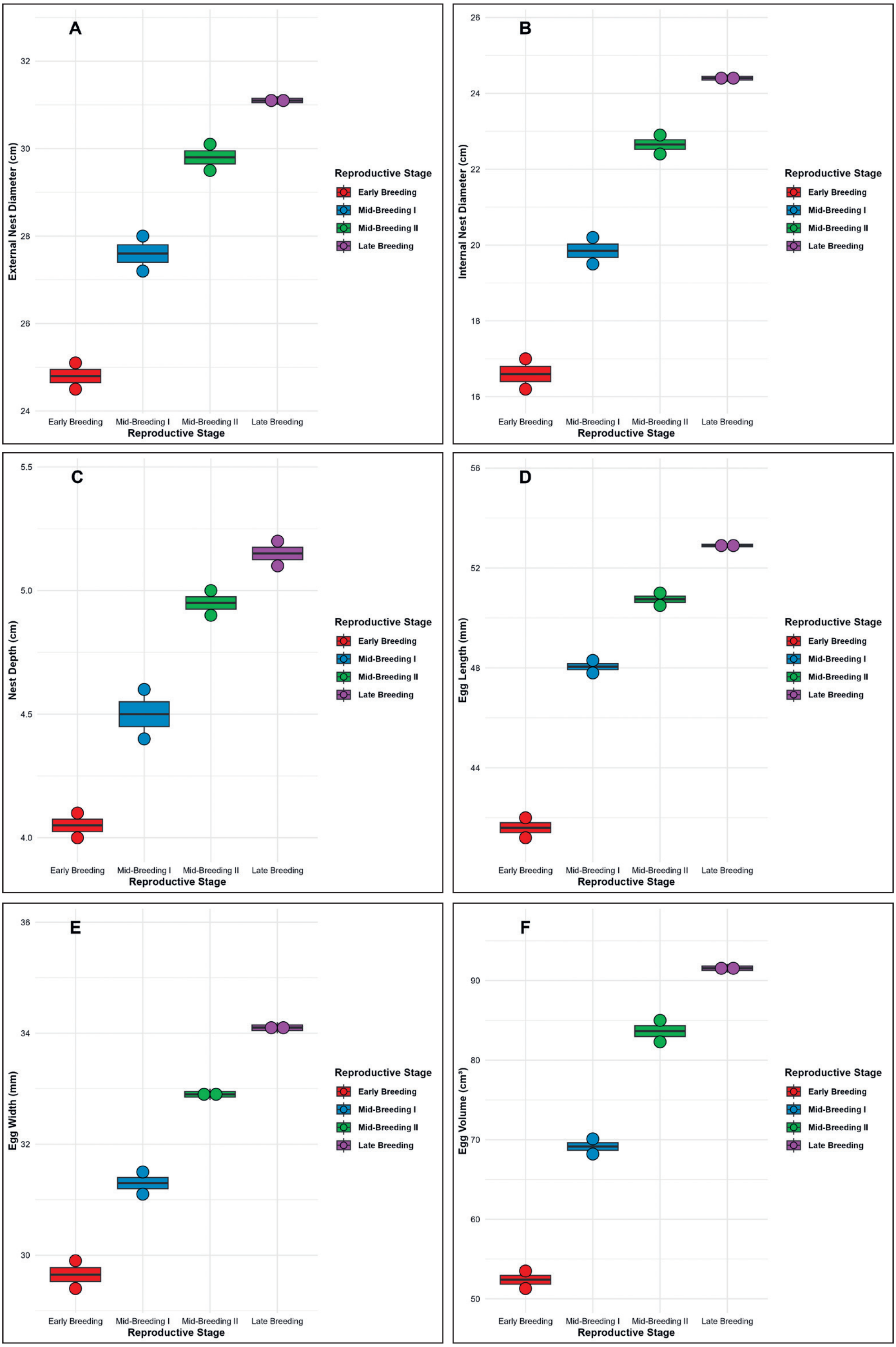
### Reproductive stages effects on morphological and reproductive parameters

Reproductive stages, defined by environmental conditions such as temperature, rainfall, and food availability, were associated with variation in nest characteristics (e.g. dimensions, structure) and reproductive parameters (e.g. egg size, clutch size, and chick survival), indicating that these traits differed across reproductive events. Post-hoc Tukey HSD tests revealed specific pairwise differences. For external nest diameter (cm, n=40 per stage), significant decreases were observed during the pre-breeding stage compared to the chick-rearing phase (diff = -0.226, $p < 0.001$). Significant differences among reproductive stages were observed in nearly all measured parameters, with consistently lower values recorded during the pre-breeding stage compared to subsequent phases. External nest diameter was significantly smaller during the laying (diff = -0.107, p = 0.008) and incubation stages (diff = -0.184, $p < 0.001$) than during chick rearing *(Figure 2A)*. Similarly, internal nest diameter values were significantly reduced in the pre-breeding stage compared to chick rearing (diff = –0.385, $p < 0.001$), laying (diff = -0.179, p = 0.005), and incubation (diff =-0.311, $p < 0.001$) *(Figure 2B)*. Nest depth showed a significant effect of reproductive stage, being lowest during pre-breeding and highest during chick rearing *(Table 1, Figure 2C)*.

Egg length varied significantly across reproductive stages, being smaller during laying and incubation compared to chick rearing *(Table 1, Figure 2D)*, while egg width also decreased significantly during pre-breeding in comparison to chick rearing (diff = -0.140, $p < 0.001$), laying (diff = -0.054, p = 0.009), and incubation (diff = -0.104, $p < 0.001$) *(Figure 2E)*. As a result, egg volume was markedly reduced during pre-breeding relative to chick rearing (diff = -0.558, $p < 0.001$), laying (diff = 0.277, $p < 0.001$), and incubation (diff = -0.468, $p < 0.001$) *(Figure 2F)*. Egg weight followed a similar trend, with significantly lower values in pre-breeding than in chick rearing (diff = -0.371, $p < 0.001$), laying (diff = -0.158, p = 0.003), and incubation (diff =-0.285, $p < 0.001$) *(Figure 2G)*.

Hatching success varied significantly among reproductive stages, being highest during chick rearing compared to laying and incubation *(Table 1, Figure 2H)*). Similarly, breeding success was significantly reduced during pre-breeding compared to chick rearing (diff = -0.630, $p < 0.001$), laying (diff = -0.304, $p < 0.001$), and incubation (diff = -0.510, $p < 0.001$) *(Figure 2I)*. These consistent patterns indicate that the pre-breeding stage is characterized by poorer nest quality and lower reproductive performance, whereas the chick-rearing phase corresponds to the most favorable conditions.

In contrast, clutch size did not show significant variation among reproductive stages. Due to non-normality of the data (Shapiro–Wilk test: W = 0.78, p = 0.018), a Kruskal–Wallis test


A
External Nest Diameter (cm)
24
26
28
30
32
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
Reproductive Stage
Reproductive Stage
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
B
Internal Nest Diameter (cm)
16
18
20
22
24
26
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
Reproductive Stage
Reproductive Stage
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
C
Nest Depth (cm)
4.0
4.5
5.0
5.5
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
Reproductive Stage
Reproductive Stage
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
D
Egg Length (mm)
44
48
52
56
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
Reproductive Stage
Reproductive Stage
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
E
Egg Width (mm)
30
32
34
36
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
Reproductive Stage
Reproductive Stage
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
F
Egg Volume (cm³)
50
60
70
80
90
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding
Reproductive Stage
Reproductive Stage
Early Breeding
Mid-Breeding I
Mid-Breeding II
Late Breeding

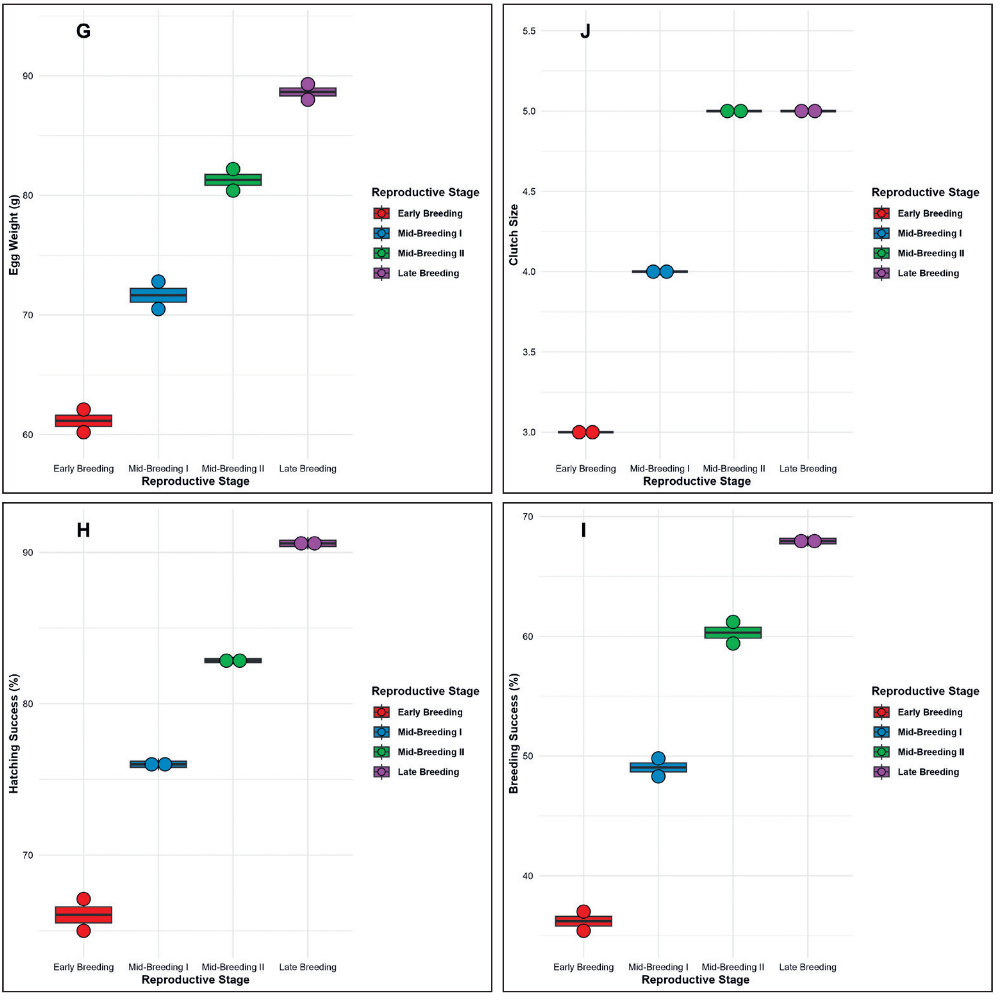



*Figure 2.* Reproductive stages effects on nest characteristics, egg traits, and reproductive success with corresponding figures: external nest diameter *(Figure 2A)*, internal nest diameter *(Figure 2B)*, nest depth *(Figure 2C)*, egg length *(Figure 2D)*, egg width *(Figure 2E)*, egg volume *(Figure 2F)*, egg weight *(Figure 2G)*, hatching success *(Figure 2H)*, breeding success *(Figure 2I)*, and clutch size *(Figure 2J)*

*2. ábra* Szezonális hatások a fészek jellemzőire, a tojások tulajdonságaira és a szaporodási sikerre: külső fészekátmérő *(2A ábra)*, belső fészekátmérő *(2B ábra)*, fészek mélysége *(2C ábra)*, tojás hossza *(2D ábra)*, tojás szélessége *(2E ábra)*, tojás térfogata *(2F ábra)*, tojás tömege *(2G ábra)*, kelési siker *(2H ábra)*, szaporodási siker *(2I ábra)* és fészekalj mérete *(2J ábra)* was applied, revealing no significant differences among stages ($\chi^2 = 7.00$, df = 3, p = 0.072) *(Figure 2J)*. This suggests that reproductive stages have minimal or no effect on the number of eggs laid per clutch in this population.

All results are summarized in *Table 1*, which includes mean values, standard deviations, sample sizes, and statistical comparisons for each parameter across reproductive stages.

*Table 1.* Summary of statistical analyses examining the effect of reproductive stages on nest morphology, egg traits, and reproductive performance in the Yellow-legged Gull *(Larus michahellis)* at Oued Charef Dam (Algeria)

*1. táblázat* A reproduktív szakaszoknak a fészekmorfológiára, a tojások tulajdonságaira és a reprodukciós teljesítményre gyakorolt hatását vizsgáló statisztikai elemzések eredményei a sárgalábú sirály *(Larus michahellis)* esetében a vizsgálati területen

| Variable | N | Test | df | F / $\chi^2$ | p-value | Post-hoc / Significant differences | Significance |
|---|---|---|---|---|---|---|---|
| external nest diameter (cm) | 40 | ANOVA | 3, 36 | 86.96 | 0.0004 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI** | *** |
| internal nest diameter (cm) | 40 | ANOVA | 3, 36 | 131.1 | 0.0002 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI**, LB > MBII*, MBII > MBI** | *** |
| nest depth (cm) | 40 | ANOVA | 3, 36 | 55.0 | 0.0010 | LB > EB**, MBII > EB**, MBI > EB*, LB > MBI** | ** |
| egg length (mm) | 40 | ANOVA | 3, 36 | 325.9 | <0.001 | LB > EB***, MBII > EB***, MBI > EB***, LB > MBI***, LB > MBII*, MBII > MBI** | *** |
| egg width (mm) | 40 | ANOVA | 3, 36 | 122.3 | 0.0002 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI**, LB > MBII*, MBII > MBI** | *** |
| egg volume ($cm^3$) | 40 | ANOVA | 3, 36 | 280.4 | <0.001 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI***, LB > MBII*, MBII > MBI** | *** |
| egg weight (g) | 40 | ANOVA | 3, 36 | 164.7 | 0.0001 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI***, LB > MBII*, MBII > MBI** | *** |
| hatching success (%) | 40 | ANOVA | 3, 36 | 292.7 | <0.001 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI***, LB > MBII**, MBII > MBI** | *** |
| breeding success (%) | 40 | ANOVA | 3, 36 | 345.6 | <0.001 | LB > EB***, MBII > EB***, MBI > EB**, LB > MBI***, LB > MBII**, MBII > MBI** | *** |
| clutch size | 40 | Kruskal–Wallis | 3 | $\chi^2$ = 7.00 | 0.0719 | EB < LB (ns), others ns (Dunn test) | ns |

***Legend**:* N = total number of nests observed (n=40), LB = late breeding, EB = early breeding, MBI = mid-breeding I, MBII = mid-breeding II**,** Significance codes**:** *** p < 0.001, ** p < 0.01, * p < 0.05, ns = not significant. Post-hoc **/** Significant differences indicate pairwise comparisons between reproductive stages (Tukey HSD for ANOVA, Dunn test for Kruskal–Wallis).

**Multivariate analysis of nesting and reproductive parameters across reproductive stages**

The results from both Principal Component Analysis (PCA) and Redundancy Analysis (RDA) revealed a strong and consistent influence of reproductive stages on nesting and reproductive traits. The first PCA axis (Dim.1), which explained 98.9% of the total variance, was highly correlated with nearly all continuous variables, especially egg volume ($r = 0.9996$, $p < 0.001$), breeding success ($r = 0.9994$, $p < 0.001$), external nest diameter ($r = 0.9911$, $p < 0.001$),clutch size ($r = 0, 9770$, $p < 0.001$),egg length ($r = 0.9882$, $p < 0.001$), egg weight ($0.9971$, $p < 0.001$), egg width ($r = 0.9882$, $p < 0.001$), and hatching success ($r = 0.9671$, $p = 0.003$). This axis represents a composite gradient of nest quality

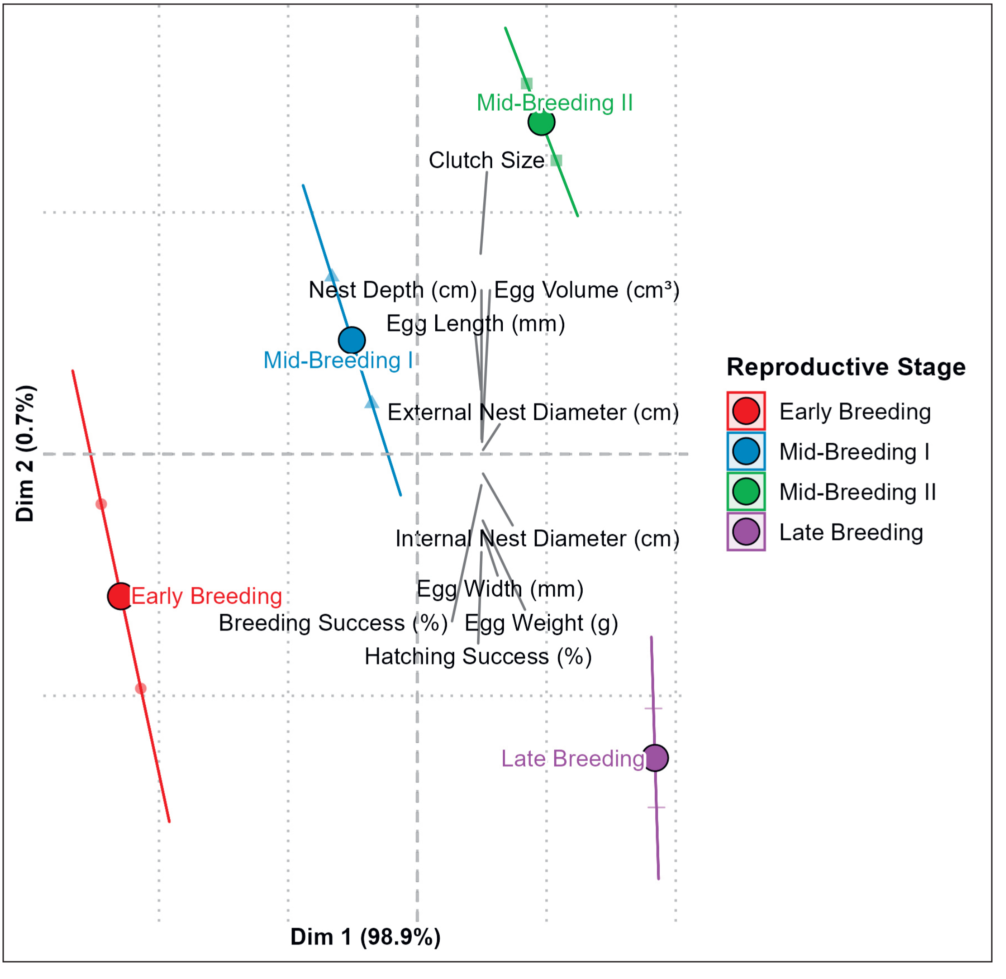



*Figure 3.* Principal Component Analysis (PCA) of nesting and reproductive traits across reproductive stages

*3. ábra* A szezonális fészkelési és szaporodási tulajdonságok főkomponens analízisének (PCA) eredményei

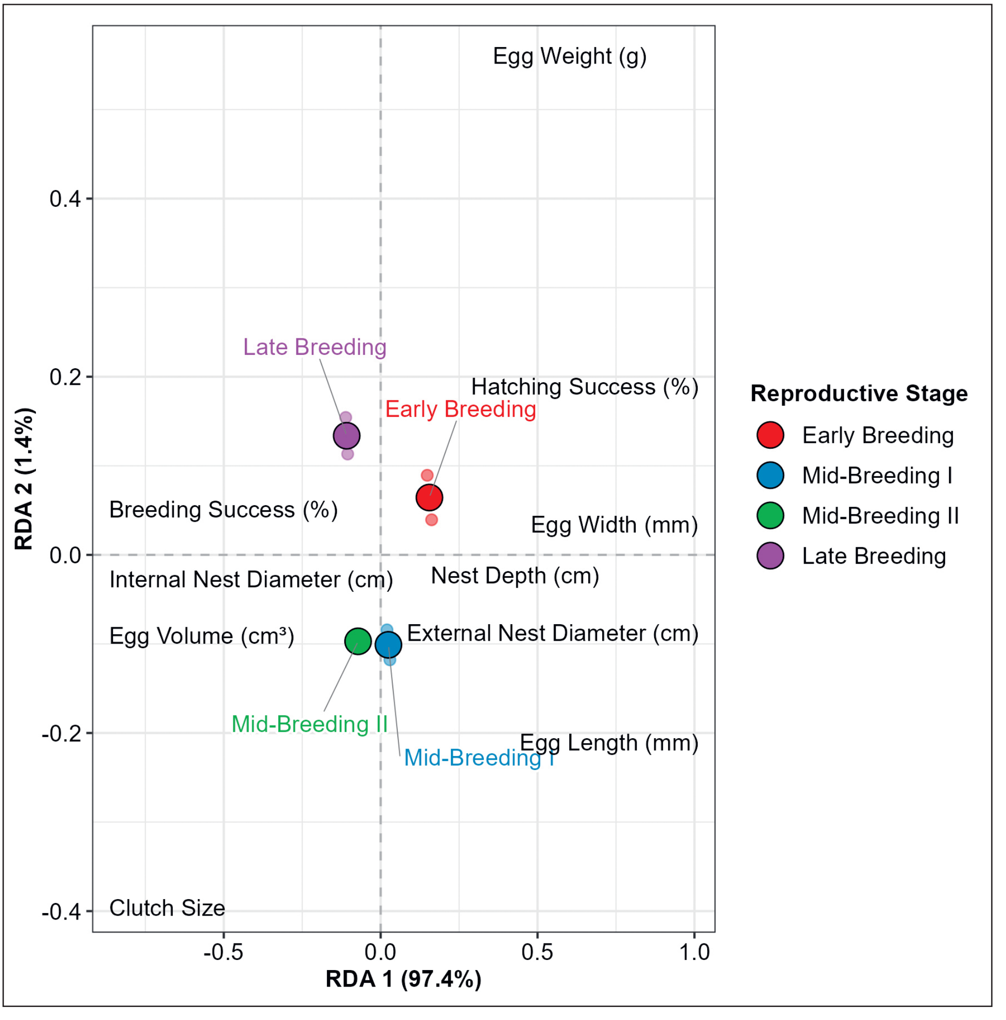



*Figure 4.* Redundancy analysis of nesting and reproductive traits of Yellow-legged Gulls
*4. ábra* A fészkelési és szaporodási jellemzők redundanciaelemzése a szezonok között

and reproductive output. Importantly, the grouping of mid-breeding I, mid-breeding II, and late breeding along this axis suggests that these stages are associated with the highest levels of reproductive performance and nest investment, while Early breeding is positioned on the opposite side of the gradient, indicating significantly lower values for these traits *(Figure 3)*.

For example, parameters such as egg width, egg weight, and hatching success show clear shifts across reproductive stages, with lower values during early breeding and higher values during late breeding, confirming the gradient revealed by the first principal component. The coplot further reveals the spread and variability within each stage, highlighting potential overlaps or distinct clusters that align with the PCA grouping.

The redundancy analysis (RDA) confirmed that Reproductive Stages explained a substantial proportion of the variation in the multivariate dataset ($R^2 = 0.994$, $p < 0.001$).

RDA1 was mainly driven by negative loadings of breeding success (-0.162), egg volume (-0.141), and clutch size (-0.031), further highlighting the gradient from low (early breeding) to high (mid-breeding I, mid-breeding II, and late breeding) reproductive investment. The ordination diagram also showed clear separation of stages along the RDA axes, with early breeding clearly isolated from the other periods. These multivariate analyses confirm that reproductive stages are a key determinant of both nesting structure and reproductive success in the studied population *(Figure 4)*.

## Discussion

This study provides novel and valuable insights into the influence of reproductive stages on nesting morphology and reproductive success in a bird population inhabiting the small island of Oued Charef Dam, northeast Algeria. To the best of my knowledge, this is the first comprehensive investigation of how environmental variation in this semi-arid Mediterranean ecosystem shapes key reproductive parameters and nesting behavior. The consistent pattern of reduced nest size (external and internal diameter, nest depth) during the early breeding stage suggests that birds invest less in nest construction when environmental conditions are less favorable. This is likely linked to lower availability of suitable nesting materials or energy conservation strategies preceding the energetically demanding breeding period (Martin 1995, Hansell 2000). Smaller nests might also reduce detection by predators during vulnerable early stages, although this trade-off requires further investigation. Similar patterns in nest morphology have been reported in Mediterranean passerines, indicating that this strategy might be widespread in habitats with marked seasonal variation (Bensch & Hasselquist 1992).

Egg characteristics, including length, width, volume, and weight, followed the same trend, with significantly smaller eggs produced during the early breeding stage. This reduction likely reflects constraints on female physiological condition and resource availability early in the reproductive cycle (Lambrechts *et al.* 1997, Borgmann *et al.* 2013). Producing smaller eggs could influence chick development and survival, as egg size is positively correlated with offspring fitness in many bird species (Encabo *et al.* 2002). The unchanged clutch size, despite smaller eggs, indicates a potential trade-off strategy where females favor producing more eggs rather than investing in egg quality under resource constraints (Williams 1994, Martin 1995). Hatching and breeding success were markedly lower during early breeding, reflecting the cumulative effects of reduced nest quality and smaller egg size.

These results are consistent with the notion that timing reproductive efforts to coincide with optimal environmental conditions maximizes fitness (Perrins 1970). The positive correlation between larger nest dimensions, increased egg volume, and higher reproductive success observed during mid-breeding I, mid-breeding II, and late breeding stages supports this adaptive timing. Comparable findings have been reported in temperate and Mediterranean species, where reproductive output peaks during periods of high food availability and moderate climatic conditions (Verhulst *et al.* 1997, Visser *et al.*

2006). Interestingly, clutch size remained stable across reproductive stages, indicating that while females adjust investment per egg and nest effort, total reproductive output in terms of egg numbers remains consistent. This pattern aligns with findings in other passerines, suggesting that clutch size may be more genetically fixed or constrained by other ecological factors (Lambrechts *et al.* 1997, Capilla-Lasheras *et al.* 2017b).

The principal component and redundancy analyses provided a powerful multivariate framework to understand how reproductive stages integrate morphological and reproductive traits into a clear gradient of reproductive investment. The stark contrast between early breeding and later stages emphasizes the importance of reproductive stage as a key driver of reproductive strategies. In Mediterranean ecosystems, where environmental conditions can change rapidly and unpredictably, such plasticity may be crucial for population persistence (Bensch & Hasselquist 1992, Both *et al.* 2006). These findings highlight the adaptive nature of reproductive timing and investment in response to environmental variability. The lower reproductive success observed during early breeding may reflect an evolutionary bet-hedging strategy, where birds reduce investment under uncertain conditions to conserve resources for more favorable periods (Perrins 1970, Martin 1995).

However, with ongoing climate change potentially altering the timing and severity of environmental conditions, these finely tuned strategies might be disrupted, leading to mismatches between breeding effort and resource availability (Both *et al.* 2006, Visser *et al.* 2006, McRae 2024). This underlines the importance of long-term monitoring of reproductive phenology and success in Mediterranean and semi-arid avian populations. While this study rigorously documents variation across reproductive stages, it is limited by its observational design and lack of detailed environmental covariates such as temperature, precipitation, and food abundance.

In conclusion, reproductive stages were strongly associated with variation in nest characteristics and reproductive performance, with the early breeding stage showing consistently lower nest quality and reduced reproductive success compared to mid-breeding I, mid-breeding II, and late breeding stages. These results underscore the influence of reproductive stages on investment strategies, reflecting how birds adjust nest morphology and reproductive effort in response to environmental and physiological constraints. Future work should incorporate experimental manipulations, such as variation in nest materials or supplemental feeding across reproductive stages, to provide causal evidence for the mechanisms driving these patterns. Additionally, investigating potential carry-over effects of early-stage reproductive constraints on offspring survival and recruitment would improve our understanding of population dynamics and life-history strategies in this semi-arid Mediterranean ecosystem. Long-term monitoring across multiple reproductive cycles will be essential to assess how environmental variability and climate change may disrupt these finely tuned reproductive strategies.

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